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Success of managed realignment for the restoration of salt-marsh biodiversity: preliminary results on ground-active spiders

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Abstract. Since the early 1990s managed realignment, where formerly reclaimed land is re-exposed to tidal inundation through breaching of coastal embankments, has been increasingly used throughout Northern Europe as a cost effective and sustainable response to biodiversity loss and flood management. This study aimed to evaluate the success of managed realignment schemes that resulted in salt-marsh development for the restoration of spider assemblages. Restoration of salt-marsh fauna was studied by comparing ground-active spiders between recently inundated land (3–14 years old) and pair-matched, adjacent natural salt marshes. Natural reference salt marshes were characterized by a relatively low species richness, the dominance of late-successional stage species such as *Pirata piraticus* (Clerck 1757), and the presence of species preferring a closed vegetation canopy like *Arctosa fulvolineata* (Lucas 1846) and *Pardosa nigriceps* (Thorell 1856). Restored habitats were characterized by greater species richness than in reference habitat and by the presence of halophilic species (*Enoplognatha mordax* (Thorell 1875) and *Erigone longipalpis* (Sundevall 1830)) and abundance of *Pardosa purbeckensis* (Westring 1861). These preliminary results argue for maintaining a maximum of successional stages in salt marshes, as they increase the diversity of halophilic spiders.

Keywords: Araneae, habitat restoration, ecological succession, halophilic species

For centuries, coastal habitats have been impacted by human activity where over-exploitation, habitat modification and pollution have led to loss of biodiversity and ecological resilience (Lotze et al. 2006). Changing climate and weather patterns have accelerated losses in the recent past (van der Wal & Pye 2004). Replacing coastal habitats where they are eroded, inundated or otherwise impacted is particularly important given the high level of ecosystem service they provide. Salt-marsh creeks provide spawning and nursery areas for many fish species and their vegetation provides roosting, nesting and feeding sites for birds. In addition to the specialist flora and fauna directly associated with tidal salt marshes they are areas of high productivity providing a source of organic matter and nutrients for adjacent marine habitats. Since the early 1990s, restoring tidal inundation to formerly reclaimed land, either through a breach in current coastal defences or whole scale embankment removal (managed realignment), has been increasingly used throughout Europe as a cost effective and sustainable response to biodiversity loss and flood management (French 2006).

Re-establishing self-sustaining plant communities are often a primary goal of such restoration efforts as these communities perform many of the biological and economically desirable functions of wetland ecosystems. Results from several managed realignment schemes have shown that with fairly minimal pre-treatment and management by allowing tidal ingress through a simple, relatively small breach, the landward realignment of coastal defences will quickly produce intertidal mudflats on low-lying agricultural land (Garbutt et al. 2006). If the elevation is suitable, mud flats will be colonized by salt-marsh plants. Monitoring programs to date have focused on the restoration of some functions, in particular sediment dynamics, plant colonization, and bird usage (Wolters et al. 2005a), but at the moment nothing is known about the restoration of terrestrial arthropod communities. This fauna represents a special conservation interest as it is currently endangered by numerous direct or indirect human impacts such as diffuse soil pollution from adjacent cultivated fields, eutrophication, and overgrazing (see the review of Adam 2002).

This study aimed to evaluate the success of managed realignment for the restoration of salt-marsh biodiversity and in particular the response of one arthropod community (*Araneae*), which constitutes a major component of the salt-marsh arthropod fauna (e.g., Meijer 1980; Pétillon et al. 2007). Ecological succession is defined as a non-seasonal, directional pattern of species change (Morin 1999). Vegetation succession in salt marshes is the result of the accumulation of nutrients in the soil leading to an increase in plant biomass and changes in species composition (Olff et al. 1997) and the frequency of tidal inundation as determined by elevation. The responses of plants to the habitat conditions found along successional gradients are well known, but few data are available on responses of arthropods. According to current theories on ecological succession and former results on salt-marsh vegetation (e.g., Olff et al. 1997), we expect (i) greater spider species richness in natural sites than in restored sites (i.e., increase in this parameter towards a climax) and (ii) differences in spider populations between natural and restoration sites (i.e., changes in species abundances along successional stages). Both hypotheses will be tested in this preliminary study by comparing ground-active spider assemblages between land recently re-exposed to tidal inundation (3–14 year old) and pair-matched natural salt marshes.

METHODS

Sampling design.—The present study was carried out in the English county of Essex (S.E. England, UK). Sites breached as

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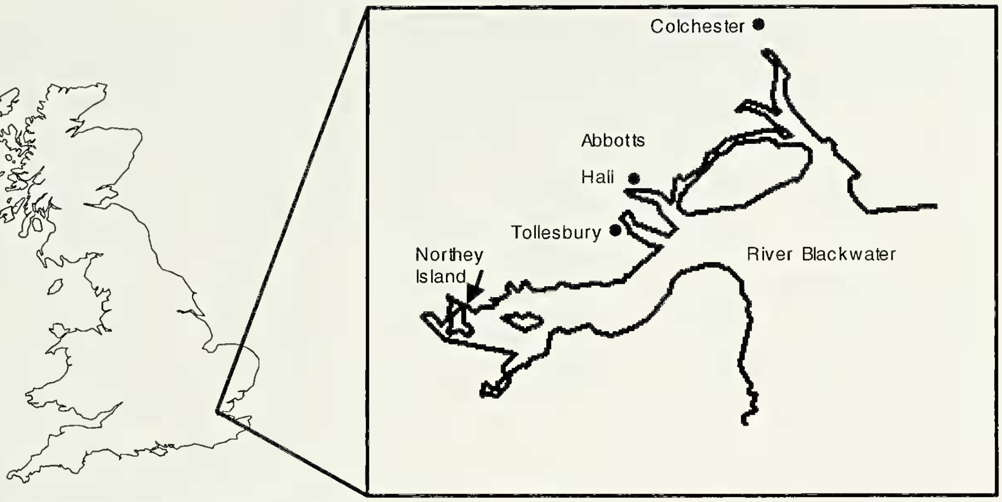

Figure 1.—Location of the 3 study sites (each site contains both restored and natural habitats) along the Blackwater River estuary (English county of Essex, UK).

part of managed realignment schemes were sampled in June 2005 giving several examples of salt-marsh development on former agricultural land. Along the Blackwater River estuary, three sites were selected because they had adjacent, natural areas (Fig. 1): Abbotts hall (Site A, 51°47′10″N, 0°51′00″E, breached 3 years ago), Tollesbury (Site B, 51°45′40″N, 0°50′00″E, breached 10 years ago), and Northey Island (Site C, 51°43′00″N, 0°43′00″E, breached 14 years ago). Sites were arranged as matched pairs with each managed realignment site (coded R for restored site) having an adjacent reference marsh (coded N for natural site) at the same elevation. The natural salt marshes, adjacent to the managed realignment sites, were only separated by the remains of the old embankment and connected by the same creek network.

Spider sampling.—Cursorial spiders were sampled with pitfall traps, consisting of polypropylene cups (8 cm diameter) with ethylene-glycol as preservative. Ten pitfall traps were installed along a 100 m long-transect at each site. Transects were placed at the same elevation (± 0.01 m) within the managed realignment site as that of the adjacent reference marsh using a laser theodolite. The elevation was selected by determining the range of the natural reference marsh by topographic survey, then selecting an elevation at random. Transects were placed parallel to the embankment and were centered on the original breach in the seawall. Elevation was used as a surrogate for tidal inundation to ensure that the arthropod communities within the managed realignment sites and reference marshes received equivalent submergence frequencies, and was checked by observing the depth and extent of the incoming tide for each site. No differences were observed. Pitfall traps were spaced 10 m apart, this being considered to be the minimum distance for avoiding interference between traps (Topping & Sunderland 1992). Data used in this study concerned the first dates of trapping in 2005 from 3–6 June. Catches in pitfall traps were related to trapping duration and pitfall perimeter, which calculates an "activity trappability density" (number of individuals per day and per meter: Sunderland et al. 1995). All the spiders collected were preserved in 70% ethanol, transported to the laboratory for species identification and kept in the University collection (Rennes, France). Nomenclature follows Canard (2005), except for *Pardosa purbeckensis* (see complete taxonomic list: Table 1), absent from this work but now considered to be a valid species (A. Canard pers. comm.).

Data analyses.—The assessment of restoration success was conducted by comparing two conservation criteria, i) abundance of target species and ii) species richness, between newly created and natural areas. The use of stenotopic species is also recommended in studying the impact of human activities and management on arthropod communities (Samways 1993; New 1995; Dufrêne & Legendre 1997). In this study, the target species were halophilic species, defined by their preference or exclusive presence in salt-marsh habitats, and rare species belonging to the Red Data Book and/or the Review of Nationally Notable Spiders of Great Britain (both statuses from Harvey et al. 2002). Halophilic species are able to resist regular submergence by seawater (monthly in Europe) and the resulting high soil salinities (Foster & Treherne 1976; Irmler et al. 2002; Pétillon et al. 2004). Species richness is widely used as a conservation target (e.g., Noss 1990; Bonn & Gaston 2005). The success of managed realignment was assessed by applying 2-way ANOVAs (GLM) to species richness and abundances with habitat type (restored or natural), site (A, B, or C) and their interaction (habitat type*site) as factors. In case of non-normal distribution (according to Kolmogorov-Smirnov tests), mean community variables were log-transformed to meet the assumptions of these Factorial ANOVAs.

RESULTS

A total of 291 adult spiders belonging to 7 families and 27 species (see taxonomic list in Table 1) were caught in natural and restored sites in 2005. Five halophilic species were recorded during the study, including two rare species: the lycosid *Arctosa fulvolineata* and the theridiid *Enoplogntha mordax*, respectively listed as Nationally Rare (status RDB3) and Nationally Scarce (status Notable A). The comparison of species composition between restored and natural sites showed a relatively low number of species only found at the natural sites (Table 1). Nine species were shared between natural and restored sites, including the halophilic species *Pardosa*

Table 1.—Taxonomic list, conservation interest (species in bold: interest is based on habitat and/or rarity according to Harvey et al. 2002), and habitat specificity (1: species only found in natural sites; 2: species shared between natural and restored sites; 3: species only found in restored sites) of the spider species.

Species	Interest		Habitat specificity
	habitat	rarity	
Gnaphosidae			
Drassyllus pusillus (C.L. Koch 1833)			3
Linyphiidae			
Bathyphantes gracilis (Blackwall 1841)			2
Diplocephalus permixtus (O. Pickard-Cambridge 1871)			1
Erigone atra (Blackwall 1841)			3
Erigone longipalpis (Sundevall 1830)	x		3
Hypomma bituberculatum (Wider 1834)			1
Oedothorax apicatus (Blackwall 1850)			3
Oedothorax fuscus (Blackwall 1834)			2
Oedothorax retusus (Westring 1851)			3
Pocadicnemis juncea Locket & Millidge 1953			1
Silometopus ambiguus (O. Pickard-Cambridge 1905)	x		2
Tenuiphantes tenuis (Blackwall 1852)			2
Lycosidae			
Arctosa fulvolineata (Lucas 1846)	x	x	1
Arctosa leopardus (Sundevall 1833)			3
Pardosa agricola (Thorell 1856)			3
Pardosa nigriceps (Thorell 1856)			1
Pardosa prativaga (L. Koch 1870)			2
Pardosa purbeckensis (Westring 1861)	x		2
Pardosa palustris (Linnaeus 1758)			2
Pardosa pullata (Clerck 1757)			3
Pirata piraticus (Clerck 1757)			2
Trochosa ruricola (DeGeer 1778)			3
Philodromidae			
Thanatus striatus C.L. Koch 1845			2
Tetragnathidae			
Pachygnatha clercki Sundevall 1823			1
Theridiidae			
Enoplognatha mordax (Thorell 1875)	x	x	3
Robertus arundineti (O. Pickard-Cambridge 1871)			3
Thomidae			
Ozyptila simplex (O. Pickard-Cambridge 1862)			3

purbeckensis and *Silometopus ambiguus*. Twelve species were found only in restored sites, two of which were halophilic: *Enoplognatha mordax* and *Erigone longipalpis*.

GLM revealed significant effects of habitat on total number of individuals, species richness, and on abundances for most species (Table 2). Site had also a significant effect for these species, resulting in several cases of significant interactions between sampling site and habitat type. No significant differences were found between the abundances of three species in natural and restored areas, despite higher abundances of *Pirata piraticus* in natural sites. For this latter, the effect of sampling site was significant and nearly significant for *Tenuiphantes tenuis*.

Total number of individuals and total species richness were higher in restored sites than in natural ones (Fig. 2). Mean values of these parameters significantly differed between sites, being greater in restored sites. Among the most abundant species that could be compared between sites, three (*Pardosa purbeckensis*, *Oedothorax apicatus*, and *O. fuscus*) showed abundances significantly higher in restored sites than in natural ones.

DISCUSSION

Habitat age, habitat structure, and species richness.—In this study, greater species richness was found in restored sites, invalidating our first hypothesis of higher species richness in natural habitats. In accordance to the results of Hurd & Fagan (1992), we suggest that habitat structure determines ground-active spider species richness rather than successional age per se. For example, among the six species only found at natural sites, the presence of at least two lycosid species can directly be related to the presence of a dense vegetation cover: *Pardosa nigriceps*, living on low vegetation (Roberts 1987), and the rare *Arctosa fulvolineata* that inhabits the heterogeneous litter of some salt-marsh habitats (Pétillon et al. 2005a). The vegetation of the natural salt marshes sampled was characterized by a closed canopy of perennial vegetation, in contrast to the vegetation of the restored sites that had a mosaic of bare ground, annual, and perennial plants (Garbutt & Wolters 2008). Such differences may also explain that some halophilic species from young and open successional stages (e.g., *Erigone longipalpis* and *Oedothorax spp.*) were not found in natural salt marshes. In the restored sites, greater species richness would

Table 2.—Species richness, number of individuals, and abundances (number of individuals/day/meter) of the main species (more than 5 individuals) by pitfall traps. Mean parameters are compared between restored and natural habitats by GLM (Whole model: df = 54).

Source	Whole model		Site		Habitat		Habitat*Site	
Dependant variable	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Species richness	20.86	**<0.001**	25.98	**<0.001**	16.29	**<0.001**	18.02	**<0.001**
Number of individuals	37.56	**<0.001**	35.62	**<0.001**	32.67	**<0.001**	41.95	**<0.001**
Abundance of :								
Oedothorax apicatus	39.35	**<0.001**	39.35	**<0.001**	39.35	**<0.001**	39.35	**<0.001**
Oedothorax fuscus	20.91	**<0.001**	21.45	**<0.001**	22.36	**<0.001**	19.63	**<0.001**
Pardosa prativaga	0.98	0.436	0.84	0.437	1.08	0.303	1.08	0.347
Pardosa purbeckensis	19.68	**<0.001**	17.71	**<0.001**	18.14	**<0.001**	22.41	**<0.001**
Pirata piraticus	3.85	**0.005**	6.61	**0.003**	2.18	0.146	1.94	0.153
Tenuiphantes tenuis	1.34	0.261	2.62	0.082	1.47	0.230	0.00	1.000

then be related to a greater spatial heterogeneity. In the case of young successional stages with uniform habitat (e.g., intensively grazed salt marshes), a general decrease in both plant (Kleyer et al. 2003) and arthropod diversity (Pétillon et al. 2007) are observed, supporting the hypothesis that spider species richness is more determined by habitat structure than by habitat age alone. Also, as web-building species richness is expected to increase with vegetation height (Greenstone 1984), this parameter should be higher in natural habitats than in restored ones. That hypothesis will soon be tested by using data from sweep-net and vortis samplings.

Determinants of species succession in salt marshes.—The second hypothesis of differences in spider populations between natural and restored sites was proven to be valid, especially with the dominance of *Pardosa purbeckensis* in newly created salt marshes. Dominance by a single wolf spider species at the beginning of ecological succession has also been described after fire (*Pardosa saltans* Töpfer-Hofmann 2000 in an Alpine

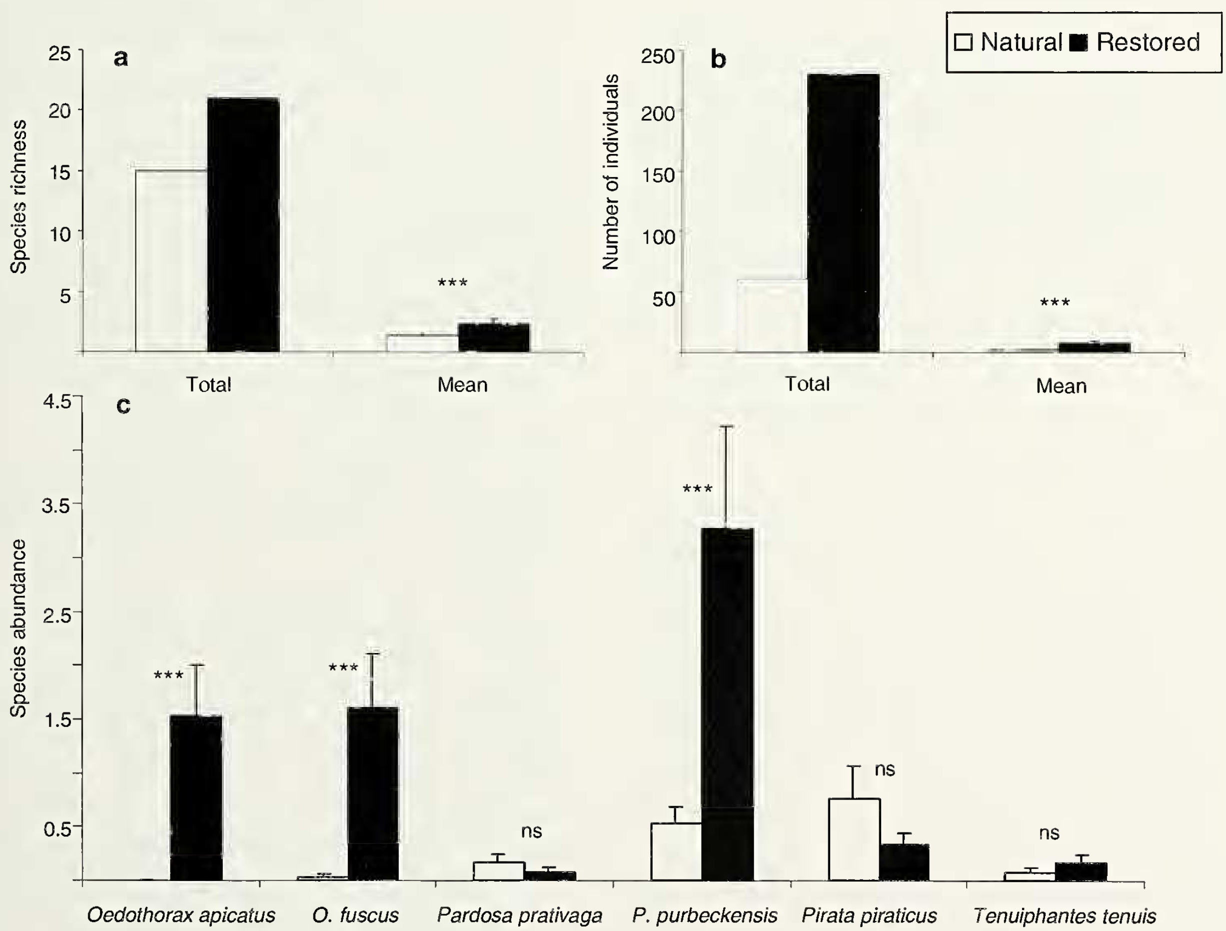

Figure 2.—Total and mean (+ 1 SE, n = 30) species richness (a), number of individuals (b) and species abundance (number of individuals/day/meter) (c) in natural and restored salt-marsh habitats. * and ** indicate significant differences by GLM ($P < 0.05$ and $P < 0.01$, respectively; for details on model results, see Table 2).

deciduous forest: Moretti et al. 2002; *Xerolycosa nemoralis* (Westring 1861) in a Finish pine forest: Koponen 2004, 2005). In salt marshes, management practices leading to younger successional stages (like sheep grazing and mowing) are known to favor some halophilic species of high interest (Zulka et al. 1997; Harvey et al. 2002; Pétillon et al. 2007) by opening soil and vegetation structures. Hurd & Fagan (1992) suggested that competition for prey is more important in early successional communities as prey is the limiting resource. Interspecific competition (and mainly intraguild predation) may explain the decrease of some species in late successional stages (Pétillon et al. 2005b). In this study, the comparison between restored and natural habitats showed an important shift in species dominance from *Pardosa purbeckensis* to *Pirata piraticus*. Such a co-existence of these two lycosids has already been reported from German salt marshes (e.g., Heydemann 1961) but does not seem to occur in France (Pétillon et al. 2006). That poses the question of interactions of ground-living spiders in these structurally simple ecosystems (Marshall & Rypstra 1999), depending on successional stages. There is thus a high interest in studying competition and predation between *P. purbeckensis* and *P. piraticus* in different salt-marsh habitats because previous studies have shown differences in the interactions between both species: null (Shaefer 1974), negative for *P. purbeckensis* (Wise 1993) and positive for *P. purbeckensis* (Pétillon pers.obs.).

Synthesis and perspectives.—The natural salt marshes were characterized by a relatively low species richness, the dominance of late-successional stage species such as *Pirata piraticus*, and the exclusive presence of large species preferring a closed vegetation canopy like *Arctosa fulvolineata* and *Pardosa nigriceps*. Restored habitats were characterized by greater species richness than the adjoining reference habitats, at least during the first years of succession. This is probably due to a more heterogeneous habitat, favoring pioneer species (mainly linyphiids). Restored habitats were also suitable for some halophilic species, in terms of both presence (*Enoplognatha mordax* and *Erigone longipalpis*) and greater abundance (*Pardosa purbeckensis*). Although these results need to be confirmed by a long-term survey, they argue for maintaining a maximum of successional stages in salt marshes as they increase the diversity of halophilic spiders.

Some ecological points need to be studied in more detail. Salt-marsh plants have been found to be effective in colonizing managed realignment sites, albeit predominantly over short distances from the local species pool (Wolters et al. 2005b). In contrast, dispersal has proved to be a critical element of arthropod patterns (e.g., Den Boer 1970). Habitat isolation and size, as well as the fauna of the surrounding habitats (Meijer 1980), could then influence habitat colonization by spiders, leading to different successional patterns in species richness between plants and arthropods. As shown by significant interactions between sites and habitats, this study needs to be completed by studying more specifically the influence of time on restoration success (by considering separately young succesional stages) and the influence of colonization process (i.e., relationships between local, regional species pool and dispersal means, especially for poor-disperser and rare species such as *Arctosa fulvolineata*).

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LITERATURE CITED

Adam, P. 2002. Saltmarshes in a time of change. Environmental Conservation 29:39–61.

Bonn, A. & K.J. Gaston. 2005. Capturing biodiversity: selecting priority areas for conservation using different criteria. Biodiversity and Conservation 14:1083–1100.

Canard, A. 2005. Catalogue of spider species from Europe and the Mediterranean basin. Revue Arachnologique 15:1–408.

Den Boer, P.J. 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). Oecologia 4:1–28.

Dufrêne, M. & P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

Foster, W.A. & J.E. Treherne. 1976. Insects of marine saltmarshes: problems and adaptations. Pp. 5–42. *In* Marine Insects. (L. Cheng, ed.). North-Holland Company, Amsterdam.

French, P.W. 2006. Managed realignment - The developing story of a comparatively new approach to soft engineering. Estuarine and Coastal Shelf Science 67:409–423.

Garbutt, R.A., C.J. Reading, M. Wolters, A.J. Gray & P. Rothery. 2006. Monitoring the development of intertidal habitats on former agricultural land after the managed realignment of coastal defences at Tollesbury, Essex, UK. Marine Pollution Bulletin 53:155–164.

Garbutt, A. & M. Wolters. 2008. The natural regeneration of salt marsh on formerly reclaimed land. Applied Vegetation Science 11:335–344.

Greenstone, M.H. 1984. Determinants of web spider diversity: vegetation structural diversity vs. prey availability. Oecologia 62:299–304.

Harvey, P.R., D.R. Nellist & M.G. Telfer. 2002. Provisional Atlas of British Spiders (Arachnida, Araneae). Volumes 1 & 2. Biological Records Centre, Huntington, Cambridgeshire, UK. 406 pp.

Heydemann, B. 1961. Untersuchungen über die Aktivitäts- und Besiedlungsdichte bei epigäischen Spinnen. Verhandlungen der Deutschen Zoologischen Gesellschaft Saarbrücken 1961:538–556.

Hurd, L.E. & W.F. Fagan. 1992. Cursorial spiders and succession: age or habitat structure? Oecologia 92:215–221.

Irmler, U., K. Heller, H. Meyer & H.-D. Reinke. 2002. Zonation of ground beetles (Coleoptera: Carabidae) and spiders (Araneida) in salt marshes at the North and the Baltic Sea and the impact of the predicted sea level increase. Biodiversity and Conservation 11:1129–1147.

Kleyer, M., H. Feddersen & R. Bockholt. 2003. Secondary succession on a high salt marsh at different grazing intensities. Journal of Nature Conservation 9:123–134.

Koponen, S. 2004. Effects of intensive fire on the ground-living spider (Araneae) fauna of a pine forest. European Arachnology 2003 (D.V. Logunov & D. Penney, eds.). Arthropoda Selecta, Special Issue Number 1:133–137.

Koponen, S. 2005. Early succession of a boreal spider community after forest fire. Journal of Arachnology 33:230–235.

Lotze, H.K., H.S. Lenihan, B.J. Bourque, R.H. Bradbury, R.G. Cooke, M.C. Kay, S.M. Kidwell, M.X. Kirby, C.H. Peterson & J.B.C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809.

Marshall, S.D. & A.L. Rysptra. 1999. Spider competition in structurally simple ecosystems. Journal of Arachnology 27:343–350.

Meijer, J. 1980. The development of some elements of the arthropod fauna of a new polder. Oecologia 45:220–235.

Moretti, M., M. Conedera, P. Duelli & P.J. Edwards. 2002. The effects of wildfire on ground active spiders in deciduous forest on the Swiss southern slope of the Alps. Journal of Applied Ecology 39:321–336.

Morin, P.J. 1999. Community Ecology. Blackwell Science, Oxford, UK. 424 pp.

New, T.R. 1995. An Introduction to Invertebrate Conservation Biology. Oxford University Press, New York. 194 pp.

Noss, R.N. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4:355–364.

Olff, H., J. De Leeuw, J.P. Bakker, R.J. Platerink, H.J. Van Wijnen & W. De Munck. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. Journal of Ecology 85:799–814.

Pétillon, J., A. Georges, A. Canard, J.-C. Lefeuvre, J.P. Bakker & F. Ysnel. 2008. Influence of abiotic factors on spider and ground beetles communities in different salt-marsh systems. Basic and Applied Ecology 9:xxx–xxx. Available online at doi: 10.1016/j.baae.2007.08.007.

Pétillon, J., A. Georges, A. Canard & F. Ysnel. 2007. Impact of cutting and sheep-grazing on ground-active spiders and ground beetles in some intertidal salt marshes (Western France). Animal Biodiversity and Conservation 30:201–209.

Pétillon, J., F. Ysnel & A. Canard. 2006. Spiders as indicators of microhabitat changes after a grass invasion in salt-marshes: synthetic results from a case study in the Mont-Saint Michel Bay. Cahiers de Biologie Marine 47:11–18.

Pétillon, J., F. Ysnel, A. Canard & J.-C. Lefeuvre. 2005a. Impact of an invasive plant (*Elymus athericus*) on the conservation value of tidal salt marshes in western France and implications for management: responses of spider populations. Biological Conservation 126:103–117.

Pétillon, J., F. Ysnel, S. Le Gleut, J.-C. Lefeuvre & A. Canard. 2004. Responses of spider communities to salinity and flooding in a tidal salt marsh (Mont St-Michel Bay, France). European Arachnology 2003 (D.V. Logunov & D. Penney, eds.). Arthropoda Selecta, Special Issue Number 1: 235–248.

Pétillon, J., F. Ysnel, J.-C. Lefeuvre & A. Canard. 2005b. Are salt marsh invasions by the grass *Elymus athericus* a threat for two dominant halophilic wolf spiders? Journal of Arachnology 33:236–242.

Roberts, M.J. 1987. The Spiders of Great Britain and Ireland. Harley Books, Colchester, Essex, UK. Volume 1:229 pp.; Volume 2:204 pp.

Samways, M.J. 1993. Insects in biodiversity conservation: some perspectives and directives. Biodiversity and Conservation 2:258–282.

Schaefer, M. 1974. Experimentelle Untersuchungen zur Bedeutung der interspezifischen Konkurrenz bei 3 Wolfspinnen-Arten (Araneida: Lycosidae) einer Salzwiese. Zoologische Jahrbücher, Abteilung Systematik, Ökologie und Geographie der Tiere 101:213–235.

Sunderland, K.D., G.R. De Snoo, A. Dinter, T. Hance, J. Helenius, P. Jepson, B. Kromp, F. Samu, N.W. Sotherton, S. Toft & B. Ulber. 1995. Density estimation for invertebrate predators in agroeeosystems. Pp. 133–162. *In* Arthropod Natural Enemies in Arable Land. Volume I. Density, Spatial Heterogeneity and Dispersal. (S. Toft & W. Riedel, eds.). Acta Jutlandica, 70(2). Aarhus University Press, Aarhus, Denmark.

Topping, C.J. & K.D. Sunderland. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. Journal of Applied Ecology 29:485–491.

van der Wal, D. & K. Pye. 2004. Patterns, rates and possible causes of saltmarsh erosion in the Greater Thames area (UK). Geomorphology 61:373–91.

Wise, D.H. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge, UK. 328 pp.

Wolters, M., A. Garbutt & J.P. Bakker. 2005a. Salt-marsh restoration: evaluating the success of de-embankments in north-west Europe. Biological Conservation 123:249–268.

Wolters, M., A. Garbutt & J.P. Bakker. 2005b. Plant colonization after managed realignment: the relative importance of diaspore dispersal. Journal of Applied Ecology 42:770–777.

Zulka, K.P., N. Milasowszky & C. Lethmayer. 1997. Spider biodiversity potential of an ungrazed and a grazed inland salt meadow in the National Park 'Neusielder See-Seewinkel' (Austria): implications for management (Arachnida: Araneae). Biodiversity and Conservation 6:75–88.

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